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Why inclusive fitness can make it adaptive to produce less fit extra-pair offspring

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Abstract

Social monogamy predominates in avian breeding systems, but most socially monogamous species engage in promiscuous extra-pair copulations. The reasons behind this remain debated, and recent empirical work has uncovered patterns that do not seem to fit existing hypotheses. In particular, some results seem to contradict the inbreeding avoidance hypothesis: females can prefer extra-pair partners that are more closely related to them than their social partners, and extra-pair young can have lower fitness than within-pair young. Motivated by these studies, we show that such results can become explicable when an asymmetry in inbreeding tolerance between monogamy and polygamy is extended to species that combine both strategies within a single reproductive season. Under fairly general conditions it can be adaptive for a female to choose an unrelated social partner, but inbreed with an extra-pair partner. Inbreeding depression is compensated for by inclusive fitness benefits, which are only fully realized in extra-pair copulations. We also show that if a female has already formed a suboptimal social bond, there are scenarios where it is beneficial to engage in EPCs with less related males, and others where EPCs with more related males increase her inclusive fitness. This has implications for detecting general relatedness or fitness trends when averaged over several species.

1. Introduction

Social monogamy is the predominant mating system of birds. Ever since studies in the 1970s and 1980s showed that genetic monogamy is rare, with extra-pair young (EPY) found in the majority of socially monogamous species [1], there has been ongoing debate on whether it is only sires of extra-pair young, or also the female parents, that benefit from having extra-pair offspring [2, 3]. Recently, the inbreeding avoidance hypothesis has gained substantial attention in this context [e.g. 4-8]. The idea is that even if there is no selection for extra-pair reproduction via additive genetic value of extra-pair young (EPY) vs. within-pair young (WPY) [9], inbreeding depression is often significant [7, 10]. Females that are paired with closely related mates should thus seek extra-pair copulations (EPCs) with more distantly related males, to reduce the number of young that suffer from inbreeding depression.

The inbreeding avoidance hypothesis, like other forms of genetic benefits sought by females, predicts that extra-pair young are fitter than within-pair young [3, 7, 11]. Although not explicitly formed as an inbreeding avoidance test, it is noteworthy that an overview of EPC in several avian species did not find support for higher fitness in EPY than in WPY [12, but see 13, 14], and results from other studies have also been equivocal [3, 15]. Moreover, there are recent studies that appear to directly contradict the inbreeding avoidance hypothesis. These include cases where

1) extra-pair partners are more closely related than social partners [16-19],

2) broods sired by related partners had lower rates of extra-pair paternity (EPP) than outbred broods [20], and

3) extra-pair young seem to have lower fitness than within-pair young [21, 22].

62 Two of these studies [17, 18] take note of a recent 'rediscovery' of a fact known for more than 70
63 years [23, 24]: inbreeding avoidance is not universally favoured as soon as there is inbreeding
64 depression [review: 7]. Choosing to mate with related partners can be selectively favoured because
65 it allows more alleles identical by descent (to those of the chooser) to be transmitted to future
66 generations [25, 26]. Put another way, inbreeding increases a female's inclusive fitness [27] by
67 allowing a related male to sire more offspring.
68
69 However, if it is beneficial to mate with related extra-pair partners, it remains unclear why females
70 would not choose optimally related social partners in the first place [28]. Suggestions include
71 limited choice for related social partners early in the breeding season [18], or that social mates may
72 provide distinct types of fitness benefits, such as parental care, creating different criteria for mate
73 choice for social and extra-pair partners [28].
74
75 Motivated by the seemingly anomalous results (cases 1-3 above), we highlight the possible role of a
76 more fundamental asymmetry in mate choice for social and extra-pair mates: an old result
77 demonstrates that inclusive fitness benefits can differ between monogamous and polygamous
78 mating systems [17, 24, 29, 30]. We show that it is equally relevant to species that combine both
79 reproductive strategies within a single breeding season. This asymmetry exists irrespectively of
80 paternal care provided by the social mate and its possible interrelationship with within-brood
81 paternity losses [e.g. 31, 32]. Therefore, the potential inclusive fitness benefits a female can gain
82 from choosing a relative as a socially monogamous mate are generally lower than those that she can
83 gain from engaging in extra-pair copulations with a relative. Our results provide a framework where
84 seemingly anomalous results, even ones where EPY are more inbred and less fit than WPY, can
85 nevertheless be adaptive for mothers. They also suggest that, in a broader context, it can be difficult

to detect overall signals regarding social partner and EPP relatedness, because it can be adaptive for a female to choose either more or less related males, depending on the scenario.

2. Materials, methods and results

Our analysis of inbreeding in socially monogamous populations proceeds in three stages. Our aim is to examine potential benefits to females, and throughout, we assume that females have control over social mate choice as well as whether an extra-pair mating happens. To keep the focus on the fitness consequences of inbreeding *per se*, we also assume that males are not able to detect compromised paternity, that a male does not pay fitness costs for EPCs, and that the sex ratio is unity; see Discussion for consequences of relaxing the last two assumptions.

First we re-derive the old result that monogamous inbreeding cannot easily invade an outbred monogamous population [24, 29]. Second, we show that a female strategy of inbreeding in extra-pair contexts can invade the same population. Finally, we consider the more general situation where a female has a social partner of arbitrary relatedness (this pair having formed for any reason), and must then decide on whether to engage in EPCs.

a) Monogamous inbreeding cannot invade an outbred, monogamous population

We begin by considering an idealized population, where all individuals form monogamous bonds and there is no promiscuity. We assume that the population is initially outbred with a 1:1 sex ratio, and then investigate whether monogamous inbreeding could invade the population. Offspring fitness is normalized such that the fitness from an outbred clutch is 1, and inbreeding with a partner of relatedness r (>0) leads to fitness $1-\delta$ per clutch.

A mutant female who prefers related over unrelated males as her monogamous partner can invade the population if her inclusive fitness is higher than that of the resident, outbred females. The inclusive fitness from an outbred clutch is simply $w_o = 1$. There are no kin benefits because the mating partners are unrelated. The mutant female's inclusive fitness from an inbred clutch in an otherwise outbred population is

$$w_i = (1 - \delta) + r(1 - \delta) - r \qquad (2.1)$$

Here, the first term corresponds to the direct fitness the female gains via her offspring, while the second term is the inclusive fitness component gained through the related male. However, this gain is more than negated by a third, negative term that is the female preventing the same male from forming an outbred pair: by definition, monogamy in a population with a 1:1 sex ratio implies that by forming a bond with a related female, he must forego the fitness he could have gained with an unrelated, non-mutant female (see Discussion for relaxing the assumption, used here, that all males find a social mate). Therefore, in this context, no additional matings are available to the male regardless of the female's actions.

The condition for an inbreeding mutant female to invade an outbred, monogamous population is $w_i > w_o$, which implies

$$(1 - \delta) + r(1 - \delta) - r > 1 \Leftrightarrow -\delta(1 + r) > 0 \Leftrightarrow \delta < 0 \qquad (2.2)$$

131 This indicates that inbreeding can only invade if inbred offspring have higher fitness than outbred
132 offspring. Therefore, under the scenario given here, inbreeding cannot invade an outbred,
133 monogamous population as long as there is any inbreeding depression [see also 24, 29].

134

135 ***b) Inbreeding in extra-pair contexts can invade an outbred, monogamous population***

136 Consider again the same outbred monogamous population as in the previous example. Now we
137 investigate whether a mutant female that is socially monogamous, but engages in promiscuous
138 extra-pair copulations can invade the outbred, monogamous population. We assume that a
139 proportion 1–q of the mutant female's clutch is fathered by the social partner (relatedness $r_s = 0$),
140 and the remaining proportion q are EPY sired by a partner of relatedness r_e. For example, if a
141 female replaces one WPY with an EPY in a clutch of size N, we have q=1/N.

142

143 Now the total inclusive fitness w_p of the promiscuous mutant female is

144

145 $$w_p = (1-q) + q[(1-\delta_e) + r_e(1-\delta_e)] = 1 + qr_e - \delta_e q(1+r_e) \qquad (2.3)$$

146

147 The first term is the fitness gain obtained through WPY production. There are no other inclusive
148 fitness components from these offspring, as the social partner is unrelated to the mother. Given that
149 the female's behaviour (q) is assumed to have no effect on the extra-pair mate's offspring
150 production elsewhere (i.e. neither an increase nor a decrease of the number of offspring he fathers
151 with his own social mate – we relax this assumption in the discussion), the negative –r term from
152 equation (2.1) is not needed for the EPY component either.

153

154 The mutant strategy can invade the resident (faithful) strategy (w_o) if $w_p > w_o$, i.e. if

$$1 + qr_e - \delta_e q(1 + r_e) > 1 \quad \Leftrightarrow \quad \delta_e < \frac{r_e}{1+r_e} \tag{2.4}$$

Equation (2.4) implies that an outbred, monogamous population can be invaded by a mutant female that forms a socially monogamous bond with a non-relative, and then engages in extra-pair copulations with a related male. For example, if mating with a brother ($r_e = 0.5$) decreases offspring fitness by one quarter ($\delta_e = 0.25$), a strategy of engaging in EPCs with a brother can invade a monogamous, outbred population, because $0.25 < \frac{0.5}{1+0.5} \approx 0.33$. Note that the female using the invading strategy has 'replaced' some of her WPY with EPY that have 25% lower fitness, a seemingly maladaptive decision. However, calculating the mother's inclusive fitness based on equation (2.3), we find that

$w_p = 1 + 0.5q - 0.25q(1 + 0.5) = 1 + 0.125q$, which is greater than $w_o = 1$ for any $q > 0$. Her inclusive fitness therefore increases with each EPY, despite each of them being less fit than the WPY they are replacing.

The crucial difference between social partner mate choice and extra-pair mate choice is that monogamy (including social monogamy) prevents, by definition, the father from forming any other monogamous bonds [29], whereas EPCs do not diminish the father's alternative reproductive opportunities in the same way. This means that inclusive fitness benefits that are not accessible via monogamy become available via promiscuous matings.

It should be noted that even if the population is invaded by an inbreeding promiscuous strategy as described above, this does not change the restrictions that monogamy imposes on the social partnerships. Inclusive fitness benefits remain absent in these pairings, and females are therefore still expected to avoid inbreeding in social mate choice. The social mate may now of course engage

180 in extra-pair copulations with other females, but as the focal female's behaviour does not have a
181 direct effect on this part of her mate's fitness, this does not factor into the inclusive fitness
182 calculations that determine the evolution of female breeding behaviour.
183
184 Our model thus far captures a fundamental asymmetry between female choice of social and extra-
185 pair males. From equation (2.2) we conclude that in the presence of inbreeding depression, females
186 should choose unrelated males as their social partner. Equation (2.4) demonstrates that unless
187 inbreeding depression is very strong, females should choose related extra-pair partners, despite the
188 resulting lower fitness of the extra-pair young; this possibility should be taken into account when
189 interpreting empirical data such as that in examples 1 [16-19] and 3 [21, 22] mentioned in the
190 introduction.
191
192 ***c) EPY production when a potential extra-pair mate is either more or less related than the social***
193 ***mate***
194 Above, we derived the expectation of inbreeding tolerance in extra-pair contexts (up to moderate
195 values of δ) combining with inbreeding avoidance in social pairings. If this outcome was always
196 achieved, a female would never produce EPY with a less related mate than her social mate. In a real
197 population, however, such situations are clearly not impossible. The social mating can be inbred for
198 reasons of limited mate availability, or if choice is influenced by territory or nest site quality
199 overriding ideal outbreeding. Selection for outbreeding can also can become weakened if the
200 population is male-biased (see Discussion). The female's best option regarding EPY production
201 then depends on her relatedness to the social mate as well as that of the potentially available extra-
202 pair mate. The equations we have derived so far cannot answer this question, yet case 2 in the
203 introduction demonstrates that this is an important point to cover: Szulkin et al. [20] found that
204 there were significantly fewer EPY in inbred broods relative to outbred broods.

205

206 We now therefore examine a more general situation where a female has already (and potentially
207 suboptimally, due to e.g. social constraints) paired with a socially monogamous partner of
208 relatedness r_s, resulting in inbreeding depression δ_s. She then has the option of engaging in EPCs
209 with a male of relatedness r_e, with inbreeding depression δ_e. The question is whether her inclusive
210 fitness increases by doing so.

211

212 Since we no longer assume that all social partnerships are outbred, the social male's alternative
213 fitness outcome (that which he would have gained if he had formed a social bond with a different
214 female) is not necessarily equal to 1 (which, in equation (2.1), gave rise to the term $-r$). The
215 resulting genealogical links also make it possible that by choosing a male of relatedness r_s the focal
216 female has had an effect on another, potentially related female's fitness by restricting her social
217 pairing opportunities (and this can in turn lead to other knock-on effects on other individuals social
218 pairing patterns). We denote these inclusive fitness components combined together as w_x. The value
219 of w_x is unknown, but as we shall see, for the following analysis this is not a problem. It is only
220 relevant that w_x is not dependent on q. This independence follows from our assumption that the
221 social bond has been irreversibly formed before decisions regarding promiscuity are made.

222

223 The female's inclusive fitness is

224

225 $$w_p = (1-q)[(1-\delta_s) + r_s(1-\delta_s)] - w_x + q[(1-\delta_e) + r_e(1-\delta_e)] \qquad (2.5)$$

226

227 We can now determine the conditions under which it pays off to engage in EPCs simply by
228 differentiating equation (2.5) with respect to q. If the derivative is positive, it is adaptive to replace
229 more WPY with EPY, and vice-versa:

$$\frac{\partial}{\partial q} w_p = -(1-\delta_s) - r_s(1-\delta_s) + (1-\delta_e) + r_e(1-\delta_e) > 0 \qquad (2.6)$$

The unknown fitness component $-w_x$ vanishes in the differentiation, as it is not a function of q. Therefore, EPY production is adaptive under the condition

$$(1-\delta_e)(1+r_e) > (1-\delta_s)(1+r_s) \qquad (2.7)$$

This is equivalent to a direct comparison of the inclusive fitnesses of social and promiscuous matings. Note that the two sides of the equation differ in their subscripts only. Given that our previous equations demonstrated a fundamental asymmetry between social and extra-pair mate choice (equations 2.2 and 2.4), the symmetrical form taken by equation (2.7) may appear surprising. The reason is that the social mate choice has already been locked. The restriction on the social male's potential to form social bonds with other females has already been set, and is not affected by the female's further actions. Given that the female's total clutch size is limited, her fitness calculations simply weigh the inclusive fitness gained via an offspring with the social mate (r_s) against that gained via an alternative offspring resulting from an EPC (r_e).

Put another way, equations (2.2) and (2.4) combined describe what the female should ideally do, whereas equation (2.7) describes whether EPCs will increase her inclusive fitness regardless of whether her social mate was ideal or not. This result (equation 2.7) is in line with case 2 as described in the introduction [20]: a female paired to a related social mate has less scope to increase her inclusive fitness via inbred EPCs than one paired to an unrelated social mate. This can lead to lower rates of extra-pair paternity in broods sired by related males than in outbred broods.

The exact outcome, however, will depend on the strength of inbreeding depression (δ_s and δ_e) as well as relatedness (figure 1 shows examples using linear dependencies between δ and r; note that equation (2.7) applies whether or not this is the case). If inbreeding depression is mild, EPY production can pay off to yield kin-selected benefits with related extra-pair males (figure 1b), while if it is strong, EPY production can instead be adaptive as a way to avoid producing (very) inbred young (figure 1d). These two benefits can combine in perhaps surprising ways in intermediate cases (figure 1c), where socially outbreeding females seek to produce EPYs for the former reason, and females in closely inbred pairs seek them for the latter reason.

3. Discussion

Our results show that previous work on adaptive inbreeding, where monogamous and polygamous systems have been considered separately [24, 29, 30], naturally extends to populations where one individual can combine both strategies within a breeding season (equations 2.2 and 2.4). It has long been known that the potential for inclusive fitness effects is much higher in polygamous than monogamous species [24, 29, 30], but the link to social monogamy combined with extra-pair matings has not been made explicit.

Our basic result is that unless inbreeding depression is very strong, females should choose unrelated social partners, and any EPY should be sired by related extra-pair partners (equations 2.2 and 2.4). If inbreeding depression is strong, then females should avoid inbreeding in all matings (within or extra-pair). These results are fully analogous to those for strictly monogamous or strictly polygamous populations.

When one additionally considers that female choice is not always ideal in the context of the initial pair formation (social mates), our results suggest that the simple principle of maximizing inclusive fitness can give rise to three different patterns of social partner relatedness and the proportion of EPY in broods (figure 1).

Mild inbreeding depression makes production of inbred EPY adaptive

When inbreeding depression is relatively low, females should engage in EPCs only if they can find a partner who is more closely related to them than their social partner (figure 1b). The relatively more inbred EPY will have lower fitness, but this is compensated for by improved inclusive fitness (equation 2.7). If the social partner is a close relative, there is less scope to do this (right side of figure 1b). Therefore, related partners should have less extra-pair young, a pattern found by Szulkin et al. [20] (however, the difference was driven largerly by immigrant females in this study; inbred females and outbred locally born females did not differ in rates of EPP).

Strong inbreeding depression makes it adaptive to produce outbred EPY

If inbreeding depression is very strong, the opposite pattern is found: females should engage in EPCs only if they can find a partner who is more distantly related to them than their social partner (figure 1d; this pattern fits with the findings of Blomqvist et al. [4], although their result is complicated by quasi-parasitism as we explain below). This will help to increase direct fitness, which under strong inbreeding depression can be so severely compromised that inclusive fitness effects are not sufficient to compensate for it.

Intermediately strong inbreeding depression implies mixed outcomes

Finally, with intermediate inbreeding depression, there is an intermediate value of social mate relatedness for which it does not pay off to engage in EPCs, regardless of whether potential EPC

303 partners are of higher or lower relatedness than the social mate (figure 1c). However, females
304 experiencing either outbreeding or close inbreeding can increase their inclusive fitness by producing
305 more, or less, outbred EPY, respectively (figure 1c).
306
307 Note that in figure 1 we consider, for simplicity, situations where inbreeding depression increases
308 linearly with relatedness, but we will below return to complications with relatedness in models of
309 inbreeding. Figure 1 should thus be taken as a conceptual illustration of potential outcomes, not as
310 an exact description of natural settings.
311
312 Although current evidence is not sufficient to prove or disprove this hypothesis, results seemingly
313 compatible with all three patterns have been found in empirical studies of EPC rates (e.g. [20], [33]
314 and [4] for figure 1b, 1c and 1d respectively). Figure 1b is also in line with findings of closer
315 relatedness in EPC partners than social partners [16-19]. As a whole, our modelling supports the
316 idea of Kleven et al. [17] that kin selection and avoidance of inbreeding depression have to be
317 considered together to understand the diversity of mating patterns with respect to inbreeding.
318
319 The fact that the exact same theoretical framework can lead to these alternative outcomes also
320 implies that a simple comparison across species may not yield clear results in support of either
321 inbreeding preference or avoidance (see conclusions).
322 Below, we discuss some further implications and limitations of our analysis, as well as limitations
323 imposed on real populations in natural settings.
324
325
326
327

a) The effect of skewed sex ratios and male opportunity costs

For clarity, we have derived our main results under the simplifying assumptions of an unbiased adult sex ratio (ASR), and males paying no costs for EPCs. Here we discuss how relaxing these assumptions affects equations (2.2) and (2.4).

The assumption of an unbiased ASR meant that it is possible for all males to find a social partner. While this is in line with much earlier work and helps brings out the asymmetry between social and extra-pair matings, the assumption's validity can be questioned because socially monogamous bird populations are often known to be male-biased [34]. In that case, the assumption of the term $-r$ in equation (2.1) (and its consequences for equation 2.2) becomes invalid; the average 'cost' imposed on males by forming a social partnership is smaller, because a fraction of them would never have been able to find a mate otherwise. A male-biased ASR can therefore make it beneficial for a female to choose a related partner even for her social partner. Quantitatively, however, the situation is not changed much. If the adult sex ratio (males:females) is denoted by ρ, then a fraction $1/\rho$ of males can acquire a social partner if $\rho > 1$ (assuming all females find a partner). A simple derivation then shows that equation (2.2) generalizes to $\delta_s < \left(1 - \frac{1}{\rho}\right)\frac{r_s}{1+r_s}$, implying increased tolerance of inbreeding depression in social mate choice by females. This is very similar in form to equation (8) in [24], but with the cost of inbreeding -term replaced by the reciprocal of the sex ratio.

Second, we add the assumption that males pay a cost c for each EPC, where c is defined as the number of effective outbred matings lost, analogous to [24]. Opportunity costs are typically assumed to be linked to parental investment [35]; for a male who does not make a significant investment in the offspring, and for whom mating does not take a very long time, c is not likely to be very high. This is true even in cases where males can effectively court only a subset of all females in a population (at the extreme, a male who lives on one island of an archipelago will not be

353 'seen' by females residing on other islands); this type of restriction should not logically be included
354 in *c*, because *c* refers to the *causal* effect that EPC success has on reducing a male's success with
355 other females. The location choices, together with the consequences for which females the male
356 appears visible, have already been made, and the subsequent occurrence or non-occurrence of local
357 EPCs does not change them. In an EPC context (where parental investment by the male is low), the
358 value of *c* can only be high if another local female (not our focal one for which fitness is computed)
359 *would* be willing to mate with the focal male, but this mating does *not* happen because the focal
360 male is permanently too 'busy' with the focal female as a result of their EPC activities. Although
361 possible (if, for example, forays into neighboring territories take up so much time that some
362 territories cannot be visited), this form of male mate choice is relatively unlikely for birds who do
363 not spend the majority of their time mating, and who generally have time to develop knowledge of
364 neighbours' identities and mating status.
365
366 Still, we can consider any value of *c* in a model. Consider the possibility that a male risks losing
367 fitness via offspring with his *social* mate based on too high extra-pair effort. Then, if the sex ratio is
368 unity, the term qcr_e must be subtracted from equation (2.3) and the following invasion analysis,
369 because the inclusive fitness of the female potentially engaging in EPCs is also reduced. However,
370 if the sex ratio is biased as above, then the male partner will again only have a social partner with
371 probability $1/\rho$, and qcr_e is replaced by qcr_e/ρ. The invasion criterion of equation (2.4) then
372 becomes $\delta_e < (1-\frac{c}{\rho})\frac{r_e}{1+r_e}$, implying decreased tolerance of inbreeding depression in EPCs by
373 females. Again, this criterion is similar to that derived for social polygyny by Waser et al. [equation
374 (8) in ref. 24], with the exception that the cost-term is divided by the (male-biased) sex ratio.
375 We can now compare the criteria for the invasion of inbreeding in WPY and EPY with these more
376 general equivalents of equation (2.2) and (2.4). Consider, for example, a male biased sex ratio ρ =
377 1.2, and a cost c = 0.3. Inbreeding can invade in the context of social mate choice if $\delta_s <$

$\left(1-\frac{1}{1.2}\right)\frac{r_s}{1+r_s} \approx 0.17\frac{r_s}{1+r_s}$. Inbred EPCs can invade if $\delta_e < \left(1-\frac{0.3}{1.2}\right)\frac{r_e}{1+r_e} = 0.75\frac{r_s}{1+r_s}$. In other words, even under this scenario with a male-biased sex ratio, and significant costs to males who engage in EPCs, inbreeding tolerance in EPCs is much higher than in monogamous matings. If male opportunity costs (c) did approach 1, then this difference would disappear, but as explained above, we consider this unlikely in most cases due to low paternal investment in extra-pair young.

b) Limitations of kin recognition

Even if optimal partners were always available, recognizing kin is not a simple task for an animal [36], and this can have significant consequences for reproductive strategies [37]. It is important to bear in mind the constraints on information available to a female when interpreting our results. In natural settings, the accuracy of information regarding relatedness can vary, and the extent and accuracy of various mechanisms is an active field of study (see e.g. [38] for novel findings on olfactory detection of relatives in zebra finches).

Recognition is simple in some cases: nest mates can use familiarity as a cue that they are more closely related to each other than to random individuals in the population; however, this gives information on only a small subset of all population members. Conversely, an immigrant female may 'know' that she is on average less closely related to her neighbours than locally born females are, but based on her own status alone she is unlikely to be able to detect differences in her relatedness to various potential mates. However, if a fraction of males migrate, a female with an immigrant male as her social partner might 'know' that she could potentially have EPY with a more closely related local male, and vice-versa. There are of course other ways in which females could

conceivably gauge their relatedness to males; these will depend on the life history of the study species, and must be taken into account on a case-by-case basis.

Given that kin recognition is not likely to ever be perfect, it is useful to know how crucial the accuracy of recognition is for our results. We explore this in the supplementary material, and find our results are quite robust to the introduction of perception error.

c) Quasi-parasitism

Our derivations were made under the assumption that the female lays all EPY eggs in her own nest, implying that they take up no space in the social nest of the extra-pair male she mated with. Apart from possible opportunity costs (c), these eggs then directly add to the number of eggs the EP male would otherwise have sired, allowing for kin-selected benefits to arise. A well-known exception to this rule is quasi-parasitism (QP; [39]), where a female lays the extra-pair egg in the nest of her EPC partner. This can have significant consequences for the potential inclusive fitness benefits that can be gained through EPCs. If the brood size in the nest of the extra-pair male has an upper limit, then the EPC eggs laid in his nest might simply take up space that would have otherwise been used by WP eggs, with no overall effect on the total number of offspring sired by him. This removes (or at least reduces) the potential inclusive fitness benefits females can gain from mating with related extra-pair males [18]. Under quasi-parasitism we should then expect EPCs not to arise through kin selection, and inbreeding avoidance is predicted to prevail in WPY as well as EPY. The argument is qualitatively similar, though quantitatively weaker, if there is no strict upper limit to brood size, but raising larger broods is costly to the male parent and/or diminishes the per capita survival of brood

426 members. In general, when such effects are strong, QP may yield no net demographic benefits to
427 host males [39].
428
429 Indeed, genetically similar social pairs had higher rates of QP in a study on three species of
430 shorebirds [4]. Moreover, in a study on ground tits, females preferred more closely related extra-
431 pair partners in normal EPCs, but not in cases of QP [18].
432
433 **d) Relatedness structure**
434 We have modelled the decisions of a single female in an initially outbred population, but the
435 evolving inbreeding patterns will have consequences on population structure. It is important to note
436 that as a population becomes more inbred, coefficients of relatedness (in the context of inclusive
437 fitness) no longer directly reflect genealogical relatedness [e.g. 40-43]. None of these factors change
438 our main results as such: the binary decisions (replace a WPY with an EPY, or not) remain valid,
439 but the interpretation of r has to be made correctly in each particular case. Any process that makes
440 the population more inbred also changes coefficients of relatedness. As modelled previously, this
441 feeds back on the inclusive fitness benefits, resulting in a lower optimal level of inbreeding than
442 would be predicted if this feedback was not accounted for [43].
443
444 This does not invalidate the current analysis, which focuses on an initially outbred population.
445 Nevertheless, it is important to keep Puurtinen's [43] insight in mind: a clear avenue for future work
446 is to investigate by how much the stable optimal level of inbreeding will be lowered by the
447 coevolution between relatedness and inbreeding. The analysis will be more complicated than in [43]
448 because there is now a need to consider a population where both extra-pair and within-pair young
449 are being produced: a new generation is now composed of WPY and EPY differing in their
450 inbreeding coefficients, and the uniform inbreeding assumption of earlier work [43] no longer

451 applies. The calculation of the coefficient of relatedness (which we for simplicity and generality
452 have left as open parameters) will then depend on further features of the population, such as the
453 proportion of EPY produced (q), migration, population size and the exact link between inbreeding
454 coefficients and inbreeding depression. This future avenue is beyond the scope of our current
455 analysis.
456
457 **e) Factors affecting the fraction of EPCs (q)**
458 Our model often gives results where it is in the evolutionary interest of a female to aim for either
459 higher (up to 1, i.e. 100% EPY) or lower (0%) values of q, the proportion of extra-pair young in her
460 brood (equation 2.7, figure 1). Our model does not directly comment on how large we expect the
461 actual proportion to be, if in principle replacing every WPY with an EPY yields fitness benefits. It
462 would clearly be difficult to completely avoid WPY production given her status of being socially
463 paired to a male, and other costs of EPY production can play a role too.
464
465 Thus, in real populations, q can be affected by factors not explicitly modelled here. Firstly, different
466 females may find themselves in situations that either favour or disfavour having EPY in broods
467 (e.g., some may be suboptimally socially paired, figure 1), resulting in intermediate population-
468 wide values of q. Secondly, to provide conceptual clarity, we in our study focused on inbreeding
469 effects and female choice, thus intentionally omitting other factors that can conceivably impact
470 extra-pair paternity. The list includes correlated selection based on male fitness [44], male
471 behavioural responses to cues of lower paternity [1, 12, 32, 45], insurance against infertility [1-3]
472 and issues of genetic compatibility [3, 15]. Which sex has power to decide on whether a copulation
473 occurs is also of relevance; our model gives the baseline expectation in female preferences for
474 social and extra-pair mate choice, if inbreeding is the focal issue.
475

476 **f) Conclusions**

477 It has proven difficult to find consistently elevated EPY fitness compared with WPY. This
478 has made it difficult to settle the question of what the adaptive basis of extra-pair copulations might
479 be [1, 3, 11, 12, 15, 46]. Here we have shown that a single underlying process, that considers both
480 inbreeding depression and kin-selected benefits of inbreeding, has potential to explain a diverse set
481 of patterns found in nature that are in apparent contradiction with each other (equations 2.2, 2.4 and
482 2.7 ; figure 1). Therefore, our results have two major implications for studies of EPC adaptiveness:
483
484 First, our model highlights the rather counterintuitive possibility that producing EPY can be
485 adaptive for mothers even if they are more inbred, and their fitness is lower than WPY fitness. This
486 does not mean that extra-pair sexual behaviour is freed of all sexual conflict, however: females
487 should still be choosier than males over EPC mates, males should still try to prevent females from
488 engaging in EPCs, and females should potentially do the same to males, at least if EPCs elsewhere
489 decrease male participation in care for the current brood. These aspects of conflict remain even if
490 both sexes are selected to engage in EPCs, and if the pairing process between social mates is
491 relatively conflict-free (at least with respect to relatedness).
492
493 Second, while this provides a framework that has potential to explain seemingly contradictory
494 empirical results, figure 1 indicates that drawing conclusions from comparisons of extra-pair partner
495 relatedness, or offspring fitness across species may be more complicated than previously assumed.
496 If the same theoretical framework can lead to opposite outcomes (figure 1), it may be difficult to
497 find a clear signal in either direction. For example, a meta-analysis compiling several studies [15]
498 found no difference between extra-pair and within-pair young in survival to the next breeding
499 season, nor a significant correlation between pair genetic similarity and rates of extra-pair paternity,
500 and therefore called for new hypotheses. Similarly, another comparative study [12] found no

501 significant difference between EPY and WPY fitness, while direct negative selection (in the form of
502 decreased paternal investment) of infidelity was stronger. From this [12] concluded that EPCs are
503 unlikely to be adaptive for females, and suggest that EPCs primarily reflect sexually antagonistic
504 coevolution between males and females. Our results suggest that this need not be the case, offering
505 alternative explanations for why EPY need not be more fit or less inbred than WPY.
506
507 This does not imply that previous comparative studies that found no clear signal [12, 15] can be
508 used as direct evidence in support of our hypothesis. Likewise, the empirical patterns that motivated
509 this study (cases 1-3, introduction) are diverse enough to retain many open questions, and it would
510 be premature (and likely incorrect) to ignore the possibility that many cases are driven by other
511 processes than the one we highlight: e.g. EPY are fitter than WPY in [19]; [16] and [19] are
512 compatible with random mating with respect to relatedness in EPY contexts, and a very recent study
513 [47] also found this to be the most parsimonious interpretation of the dataset in [21] — raising the
514 possibility that kin recognition might simply be weak or absent. Thus our goal is not to claim that
515 all cases will fall into the category indicated by our title, instead our work is intended to serve as a
516 reminder that the magnitude of inbreeding depression, the availability of social mates of suitable
517 relatedness, and the magnitude of opportunity costs should all be considered on equal footing; and
518 that the last factor in particular is likely to differ between within-pair and extra-pair contexts. It also
519 suggests a novel and relatively simple answer to the question of why females should have different
520 preferences regarding their social and extra-pair partners [e.g. 28].
521
522 Our results also have implications for the stability of monogamy. If there is inbreeding depression,
523 females are often predicted to choose an unrelated social mate under both social and genetic
524 monogamy. If costs of inbreeding are not very high, this sets up a situation where females are
525 selected to engage in extra-pair copulations with related males (equation 2.4). This forms a

significant category of genetic benefits that can make monogamy vulnerable to invasion by polygynous and polyandrous mating tactics under fairly general conditions, potentially also leading to the loss of biparental care [32, 45]. This adds to the list of many reasons why females may be expected to mate multiply [11, 48].

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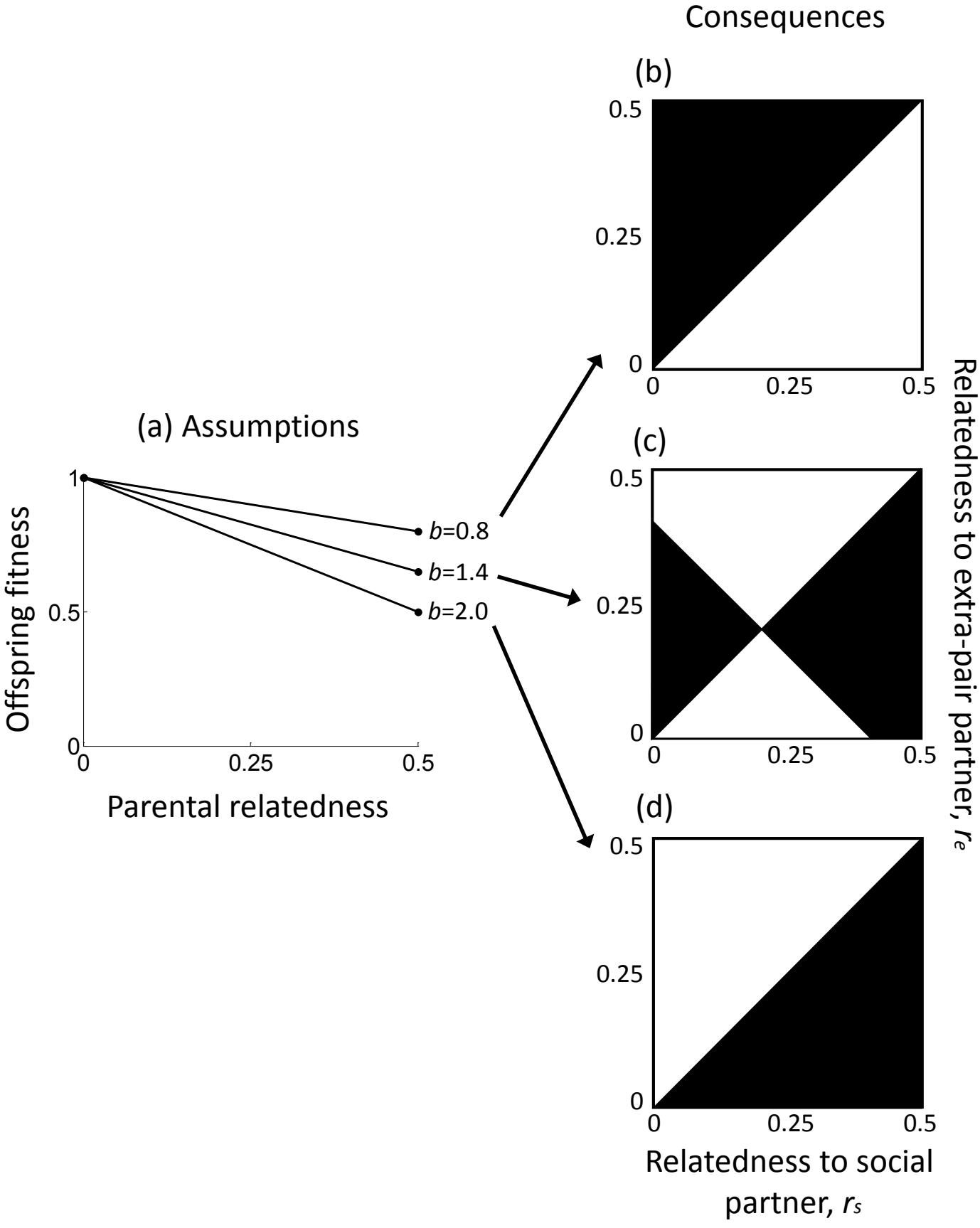
660

661

662 **Figure legends:**

663 **Figure 1.** Given that a female has paired up with a social partner of relatedness r_s, she should accept
664 EPCs with males of relatedness r_e in the sections shaded in black, but not in the white regions.
665 These arise from equation (2.7) when combined with the further assumption that inbreeding
666 depression is a linear function of relatedness ($\delta = \frac{br}{2}$), resulting in the condition
667 $\left(1 - \frac{br_e}{2}\right)(1 + r_e) > \left(1 - \frac{br_s}{2}\right)(1 + r_s)$. The result is strongly dependent on the strength of
668 inbreeding depression as depicted in panel (a). In panel (b) inbreeding depression is relatively low,
669 and females are selected to choose extra-pair partners that are more closely related to them than
670 their social partners. Therefore, EPY have lower fitness than WPY. In panel (d), high inbreeding
671 depression reverses this choice, and EPY are fitter than WPY. In the intermediate case of panel (c),
672 EPY can have either lower or higher fitness than WPY, and the crossover point indicates an
673 intermediate, optimal level of inbreeding where inclusive fitness cannot be increased by mating
674 with either a more or less related partner. This point corresponds to the optimum relatedness for
675 female mate choice in an outbred population derived previously [43].
676
677


Consequences
(b)
0.5
0.25
0
0
0.25
0.5
(a) Assumptions
1
0.5
0
Offspring fitness
b=0.8
b=1.4
b=2.0
0
0.25
0.5
Parental relatedness
(c)
0.5
0.25
0
0
0.25
0.5
(d)
0.5
0.25
0
0
0.25
0.5
Relatedness to social partner, r_s
Relatedness to extra-pair partner, r_e

The role of kin recognition

If kin recognition is not perfect, the conditional strategy does not necessarily pay off. However, it is our aim here to show that mild imperfections do not destroy the argument.

Consider equation 2.7 in a situation where the two potential sires — one assigned to already be in a social mate role, the other is the potential extra-pair mate — differ in relatedness. We denote the lower of the relatedness values by r_L and the higher as r_H, regardless of which male offers which one of these values. The corresponding values for inbreeding depression are δ_L and δ_H. To simplify the notation further, we write $A = (1 + r_L)(1 - \delta_L)$ and $B = (1 + r_H)(1 - \delta_H)$, and we write P for the probability that a female facing this situation in the population has, in reality, the lower relatedness option as her social mate; thus in a proportion $1–P$ of cases the social mate is the one to whom relatedness is higher.

We introduce unreliable assessment of relatedness by assuming that in a proportion ε of cases where a female perceives the less related male to be the more related one; a female who has made this mistake, and behaves in a way dictated by equation 2.7., will use this equation the 'wrong way', with all relatedness and inbreeding depression values swapped compared with the real situation. We now ask: does a female whose mating strategy is flexible, i.e. dictated by eqn 2.7 but with perceived rather than real relatedness, have higher expected fitness than a female who is inflexible and (i) never has any EPY, or (ii) always has a proportion q of EPY?

We first derive the inflexible females' fitness. Ignoring the w_x term in eqn 2.5 (which we can do without introducing error as it is unaffected by EPC decisions; see main text), the 'no EPY' female's fitness is simply $w_0 = PA+(1–P)B$. The 'always q' female's fitness is $w_q = P[(1–q)A+qB]+(1–P)\,[(1–q)B+qA]$. The difference between these values determines which

type of inflexible behaviour is the flexible female's most serious competitor. The difference simplifies to

$$w_0 - w_q = (B–A)\ q\ (1–2P)$$

This creates the following table for a flexible female's most serious competitor's fitness; the flexible strategy's fitness has to be higher than values in this table for it to win. (We have the $P = 0.5$ and $A = B$ cases listed separately for clarity, note however that they are equal to the neighbouring cases in the limit.)

Table S1. The fitness of the most serious competitor of a flexible female strategy, i.e. $\max\{w_0, w_q\}$

	$P < 0.5$	$P = 0.5$	$P > 0.5$
$A > B$	$P[(1–q)A+qB]+$ $(1–P)\ [(1–q)B+qA]$	$PA+(1–P)B$	$PA+(1–P)B$
A = B	$PA+(1–P)B$	$PA+(1–P)B$	$PA+(1–P)B$
A < B	$PA+(1–P)B$	$PA+(1–P)B$	$P[(1–q)A+qB]+$ $(1–P)\ [(1–q)B+qA]$

We next proceed to deriving the flexible female's fitness, denoted w_f. As stated above, this female behaves according to 2.7, but in a proportion ε of cases the decision is based on mistakes and the female uses q for its EPY proportion when 0 would have yielded better fitness, or 0 when q would have yielded better fitness. It is easiest to consider the case $A > B$ separately from $B > A$. In the former case,

$$w_f = P(1-\varepsilon)A + P\varepsilon[(1-q)A+qB] + (1-P)(1-\varepsilon)[(1-q)B+qA] + (1-P)\varepsilon B$$

$$= A\,[P(1-q)+(1-\varepsilon)q] + B\,[1-P(1-q)-(1-\varepsilon)q]$$

Note that because $q > 0$ and $A > B$ in this setting, increasing error ε always has a fitness-reducing effect regardless of the value of P.

In the latter case where $B > A$, we have

$$w_f = P\,(1-\varepsilon)\,[(1-q)A+qB] + \; P\varepsilon A + (1-P)\,(1-\varepsilon)\,B + \,(1-P)\varepsilon\;\; [(1-q)B+qA]$$

$$= A\,[P(1-q) + \varepsilon q] + B\,[1-P(1-q) - \varepsilon q]$$

Again, errors always reduce fitness.

So now the comparison: for which values of ε is it true that $w_f > \max\{w_0, w_q\}$? The corresponding inequalities are given in table S2 below for each of the 9 different possibilities that can occur.

	$P < 0.5$	$P = 0.5$	$P > 0.5$
$A > B$	$A\,[P(1-q)+(1-\varepsilon)q] + B\,[1-P(1-q)-(1-\varepsilon)q] > P[(1-q)A+qB]+ (1-P)\,[(1-q)B+qA]$	$A\,[P(1-q)+(1-\varepsilon)q] + B\,[1-P(1-q)-(1-\varepsilon)q] > PA+(1-P)B$	$A\,[P(1-q)+(1-\varepsilon)q] + B\,[1-P(1-q)-(1-\varepsilon)q] > PA+(1-P)B$
$A = B$	$A\,[P(1-q)+(1-\varepsilon)q] + B\,[1-P(1-q)-(1-\varepsilon)q] > PA+(1-P)B$	$A\,[P(1-q)+(1-\varepsilon)q] + B\,[1-P(1-q)-(1-\varepsilon)q] > PA+(1-P)B$	$A\,[P(1-q)+(1-\varepsilon)q] + B\,[1-P(1-q)-(1-\varepsilon)q] > PA+(1-P)B$
$A < B$	$A\,[P(1-q)+\varepsilon q] + B\,[1-P(1-q)-\varepsilon q] >$	$A\,[P(1-q)+\varepsilon q] + B\,[1-P(1-q)-\varepsilon q] >$	$A\,[P(1-q)+\varepsilon q] + B\,[1-P(1-q)-\varepsilon q] > P[(1-q)A+qB]+$

	$PA+(1-P)B$	$PA+(1-P)B$	$(1-P)\,[(1-q)B+qA]$

The solutions are very simple, and do not depend on q at all:

	$P < 0.5$	$P = 0.5$	$P > 0.5$
$A > B$	$\varepsilon < P$	$\varepsilon < 1/2$	$\varepsilon < 1-P$
$A = B$	$\varepsilon < P$	$\varepsilon < 1/2$	$\varepsilon < 1-P$
$A < B$	$\varepsilon < P$	$\varepsilon < 1/2$	$\varepsilon < 1-P$

This can be summarized as a single inequality: the flexible strategy wins if $\varepsilon < \min\{P,1-P\}$.

For the interpretation, consider first the case where $P = 0.5$. For an inflexible female it is then equally good to have EPY as not to have them: $P = 0.5$ offers no way of predicting whether this has an improving or damaging effect on female inclusive fitness, as relatedness is random regarding whether the potential sire is the female's social mate or not. A flexible female, on the other hand, will be able to fine-tune its behaviour according to her current social situation that differs from the population average of $P = 0.5$. As long as $\varepsilon < 1/2$, this female will tend to have EPY when it improves her inclusive fitness, and not have them when their production would have lowered inclusive fitness. Even if kin regognition is somewhat erroneous, this flexibility leads to higher fitness than either type of inflexibility, as long as the error rate does not exceed 0.5. Note that $\varepsilon = 0.5$ indicates that the female is as often right as she is wrong (i.e. completely random guess), and $\varepsilon > 0.5$ implies that the female ranks

relatedness values in the wrong order more often than in the correct one (i.e. her guess is worse than random).

Thus, if females are equally often in situations where either the within-pair male or the extra-pair male provide better inclusive fitness ($P \approx 0.5$), then our main results are remarkably robust: any degree of accuracy of kin regognition that is better than a pure guess (i.e. $\varepsilon < 0.5$) will favour the female strategy that is based on 'believing' eqn 2.7; even if assessments of relatedness are relatively frequently incorrect.

The situation changes somewhat if P deviates from 0.5, being closer to 0 or 1. If P is very low or very high, then inflexible females who do not assess the situation separately for each pairing can, despite their lack of assessment, still benefit from evolutionarily acquired knowledge: in most cases the pair mate is the high-relatedness one if P is close to 0, or in most cases he is the low-relatedness one (if P is close to 1). This means that one of the inflexible strategies (which one of them, depends on whether $A > B$ or $B > A$) can perform relatively well. The condition for the flexible strategy to beat the better one of the inflexible strategies becomes therefore more restrictive than $\varepsilon < 0.5$; if, for example, $P = 0.1$ such that social mates are much more often more closely related to the female than a potential extra-pair mate, then the female should rank kin relationships correctly 90% of the time or better, for the recognition-based strategy to work.

Note that if potential mates typically vary only little in relatedness, then achieving correct rank orders is harder and ε is then likely to be large. However, under such conditions we also have $A \approx B$ as well as $P \approx 0.5$ (as there is then no reason to assume that pair formation is strongly impacted by minute relatedness differences). The conditions for our process to work are then at their mildest, where any better than random recognition capacity, $\varepsilon < ½$, is sufficient. If potential mates vary greatly in relatedness, errors ε may have a more damaging

effect on the success of the flexible strategy, but on the other hand it is then also easier to achieve a low error rate.

Obviously, in all these cases, if there is no kin recognition mechanism in place at all, the envisaged process cannot work; some positive relation between perception of relatedness and real relatedness is always required, but our results above confirm that accuracy does not always have to be strong.